POST-LARVAL GROWTH OF *DISSODACTYLUS PRIMITIVUS* BOUVIER, 1917 (BRACHYURA: PINNOTHERIDAE) UNDER LABORATORY CONDITIONS

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ABSTRACT

Dissodactylus primitivus is a small pinnotherid crab parasitic on spatangoid urchins. Post-larval growth has been observed in the laboratory in the absence of hosts. Individual animals were grown over the whole size range of the species for a period of 691 days after hatching. During growth of *D. primitivus* males and females, there was no significant change in carapace width with length. Relative to carapace width, male abdominal width increased isometrically. Growth of the female abdomen was allometric and could not be explained by a simple relationship. Two phases leading to sexual maturity were recognized: one of low positive allometry, the other of strong allometric growth. During the latter phase pubertal molts occurred.

Growth over time showed decreasing increments and an increase in intermolt periods, with slight differences between sexes. The resulting growth rates closely fitted power curves. Compared to females, growth of males decreased after the first year. This could explain the presence of larger females in natural populations.

Several growth relationships analogous to weight were demonstrated and the results discussed in relation to other Crustacea.

INTRODUCTION

Studies of age and growth contribute to an understanding of population dynamics and to the elucidation of developmental processes. Among Crustacea, such studies have most often centered on species of commercial interest (Maucheline, 1977), including prawn (Forster, 1970; Wickins, 1976), lobster (Thomas, 1965; Ennis, 1972) and crabs (Weber, 1967). Little comparable information is available on crustacean species, especially crabs, in the low size range. *Dissodactylus primitivus* is a small pinnotherid crab with a maximum carapace width of less than 1 cm, living as a parasite on the spatangoid urchins *Meoma ventricosa* and *Plagiobrissus grandis* (Telford, 1978b, 1982).

Despite many attempts since the landmark paper by Kurata (1962) to comprehensively describe age and growth in crustaceans, one major problem has persisted. It is the difficulty of obtaining morphometric data for known-age individuals. Several studies of allometry have relied entirely on collections of wild specimens of unknown age. For example, Finney and Abele (1981) have analyzed changes of shape with size in a xanthid crab, *Trapezia ferruginea* and Williams *et al.* (1980) have compared size and shape relationships in three species of *Uca*.

Similarly, Haley (1969) was able to correlate sexual maturity with external morphology in the ghost crab, *Ocypode quadrata*, from specimens of unknown age. Growth increments at successive molts have also been estimated from individuals of unknown age. Thus Sheader (1981) described increase in size in an amphipod, *Parathemisto gaudichaudi*, from wild specimens maintained in the laboratory. Data from tagged animals released and recaptured (*e.g.* Bennet, 1974) suffer from the same inherent uncertainty. Theoretically, the solution to the problem should be simple: culture the organisms from egg or known larval instars. With known-age individuals it is possible to analyze the two principal components of growth (Needham, 1964), namely, rate and change of form (differential growth). Although considerable success has been achieved in laboratory culture of shrimps and lobsters (Bardach *et al.*, 1972), few, if any, crabs have been successfully reared in continuous culture.

We have raised *Dissodactylus primitivus* from egg to adult size, providing a series of measurements for each of the thirty or more instars for individuals of precisely known age. Post-larval growth is examined here with two major objectives: the first to observe changes in form with reference to size, the second to investigate growth as it occurs over time. Larval development is described elsewhere (Pohle and Telford, 1983). This paper on post-larval growth thus completes a developmental study of *D. primitivus*.

Materials and Methods

Collection of parental stock. Ovigerous female crabs were collected with host spatangoid urchins, *Meoma ventricosa*, from sandy bottoms in 5–18 m of water, off the western coast of Barbados. Specimens were kept in 50-liter tanks until hatching occurred. Egg masses were periodically examined for maturity and possible protozoan or fungal infection. Newly produced egg masses are bright orange in color, becoming pale yellow towards the end of maturation. Hatching of zoeae for this study occurred between 9 and 11 p.m. on June 12, 1978.

Rearing procedure. At time of hatching a numbered series of 100 of the most vigorously swimming, positively phototactic larvae were pipetted into individual 120-ml glass jars ⅔ filled with sea water. Maintenance of larvae followed procedures outlined by Pohle and Telford (1983). Post-larvae were inspected daily, given live food, and transfered to new containers with about 90 to 120 ml fresh sea water (depending on size). Measurements were taken following every molt. Animals and containers were kept in a water table of running sea water to approximate temperatures to natural conditions.

Culture medium and conditions. Sea water fed into the laboratory was found to be inadequate even when filtered. Instead, fresh sea water was collected daily about 500 m offshore. In this way filtering or addition of antibiotics were found to be unnecessary.

For the entire rearing salinity ranged from 31.5 to 34‰ (mean 33‰). Temperature varied between 26.5 and 29.5°C (mean 28°C), about 0.5 to 1.0°C above the natural environment. A 14-h photoperiod was maintained.

Food. Larvae and early post-larvae were fed with newly hatched *Artemia* nauplii *ad libitum*. In addition, selected plankton of appropriate size, collected in daily trawls, was given as a food supplement. For later stages increasingly larger *Artemia* nauplii and planktonic organisms on which crabs readily fed were used.

Measurements. At each instar, specimens were measured live, twice, and the results averaged. After molting the exuvium was also measured. No significant difference was found between exuvial and live measurements.

Imminence of molting was apparent by a change in carapace opacity 1–2 days before exuviation. Exuviae were never eaten by any of the specimens.

The following measurements were made under the light microscope by calibrated ocular micrometer: maximum carapace width, dorsally and anteriorly; carapace length from vestigial rostrum to posterior margin, ignoring curvature; and width of abdomen at its widest point.

Statistical analysis. All regression lines were fitted by least squares analysis. Its major disadvantage is that error is assumed to occur in only one of the two variates and may result in a low estimate of slope (Gould, 1975). There are several other methods (Sokal and Rohlf, 1969) which consider error in both variates, but least squares was used here following arguments given by Brown and Davies (1972), Gould (1966), and Finney and Abele (1981): (1) it is easier to interpret and allows the use of standard tests of significance; (2) since most correlation coefficients (r) in this study are above 0.90, results with other methods should not be substantially different; and finally, (3) a comparison of methods by Brown and Davies (1972), using Doryline ants, has shown differences in results to be very small. This was at least partly attributed to the particular discontinuous growth pattern of the arthropod exoskeleton, where size differences between instars are much greater than for individuals of a given instar. The same argument applies here.

Zar (1968) raised objections to the widely accepted use of log transformations of power functions, suggesting instead the use of the curvilinear non-transformed model. This problem has not yet been satisfactorily resolved (Finney and Abele, 1981), but the conventional linear transformation used here has been recommended (Sacher, 1970).

In order to study changes in growth, a reference dimension which itself shows little or no change in growth rate is selected (Brown and Davies, 1972). In brachyuran crustaceans this is usually either carapace length (*e.g.* Finney and Abele, 1981) or carapace width (*e.g.* Barnes, 1968). A regression of these two parameters is often isometric (Warner, 1977), *i.e.* without significant change in ratios during growth. Width was chosen here because carapace length in *D. primitivus* is a less reliable measurement due to curvature along the longitudinal axis.

The power function $y = ax^b$ is known to biologists as the equation of simple allometry. It has found wide application in the analysis of growth (Gould, 1966). The theoretical basis claimed for this function by Teissier (1960), however, has not been universally accepted (Kidwell and Williams, 1956), and consequently it should not be considered a fundamental law of growth (Pasternack and Gianutsos, 1969). In this study linear ($y = bx + a$), semi-log ($\log y = bx + a$), and power functions (as log-log, $\log y = b \cdot \log x + \log a$) were applied to all data and that model which combined the simplest explanation of the data with the best possible fit was chosen.

For determination of allometric status, regressions were tested against either an isometric intercept standard of 0 for linear regression, or an isometric slope standard of 1 for power functions with a Students t-test (Sokal and Rohlf, 1969). Analysis of co-variance (F-test) was employed to compare slopes. Regression lines, statistics, and bivariate scattergrams were obtained by computer from programs in the Statistical Analysis System (SAS) package.

RESULTS

Survival and mortality

In the laboratory mortality was highest during the relatively short larval life, especially the megalopa, only 44 reaching the first crab instar (Fig. 1). The number
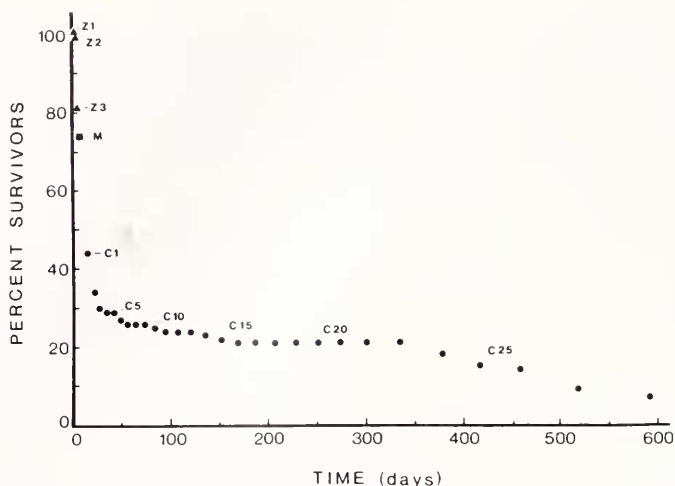
FIGURE 1. Survival of *Dissodactylus primitivus* in the laboratory. Points represent mean values for successive instars. Symbols: ▲, zoeal stages (Z1 to Z3); ■, megalopa (M); ●, post-larval instars (C1 to C28).

of survivors then gradually decreased, to 21 by instar 16 (mean day 169), with no further deaths occurring for about another ½ year (instar 23, mean day 335). Subsequently, numbers of survivors steadily decreased (a constant average mortality rate represented by points falling in a straight line) to 12 by post-larval instar 28, almost 600 days after hatching. On day 691 the rearing experiment was discontinued with 4 survivors remaining, 2 females (instars 28, 32) and 2 males (instars 28, 29).

Carapace width and length

The relationship of mean carapace widths (CW) and lengths (CL) for post-larval instars 1–28 and of individual values for two specimens which reached instars 30 and 32 (Fig. 2) was given by the equation:

$$CL = 0.828 \cdot CW + 0.036 \qquad (r^2 = 0.994)$$

This calculated line, for the two sexes together, was based on 550 pairs of measurements. For separate sexes the intercepts were not significantly different from 0 (t-statistic = 1.02, $P = 0.31$ for males; $t = 1.81$, $P = 0.07$ for females). Thus the relationship was regarded as isometric.

The difference of slope between sexes was not significant ($F = 0.35$, $P = 0.55$). Male crabs (max CW = 8.1 mm), however, never reached sizes of the largest females (max CW = 9.5 mm). These large, laboratory-reared crabs are of equal or greater size than those found in the wild (CW < 10 mm).

Carapace width and abdominal width

Based on 239 paired measurements of crabs from post-larval instars 5 to 28, the relationship of abdominal width (ABDW) and carapace width (CW) for male crabs was:

$$ABDW = 0.389 \cdot CW - 0.117 \qquad (r^2 = 0.997)$$

Fitting the data to a power function resulted in the equation:

$$\text{ABDW} = 0.309 \cdot \text{CW}^{1.010} \qquad (r^2 = 0.998)$$

Figure 3 shows a log-log transformation, where:

$$\log \text{ABDW} = 1.010 \cdot \log \text{CW} - 0.510$$

The slope of 1.01 indicated isometric growth ($t = 1.30$, $P = 0.21$).

During growth, abdominal width in females increased more in higher instars, fitting a power curve which, expressed as a log-log function, was given by the equation:

$$\log \text{ABDW} = 1.481 \cdot \log \text{CW} - 0.616 \qquad (r^2 = 0.984, \text{N} = 226)$$

Regression slopes were significantly different for the sexes ($F = 1146.10$, $P = 0.0001$).

Analysis of growth of individuals and means for instars (Fig. 3) showed that the relationship was not of simple allometry. There was a change of slope approximately between instars 19 and 20 (see arrow Fig. 3). The data were better represented by two separate regressions, for early instars:

$$\log \text{ABDW} = 1.295 \cdot \log \text{CW} - 0.548 \qquad (r^2 = 0.995, \text{N} = 157)$$

and for later instars:

$$\log \text{ABDW} = 2.025 \cdot \log \text{CW} - 1.048 \qquad (r^2 = 0.931, \text{N} = 69)$$

Both slopes were significantly greater than 1 ($t = 55.14$, $P = 0.0001$ and $t = 35.42$, $P = 0.0001$, respectively) and hence growth was not isometric but positively allometric. The two slopes were significantly different ($F = 541.33$, $P = 0.0001$), indicating markedly different growth in the two size groups.
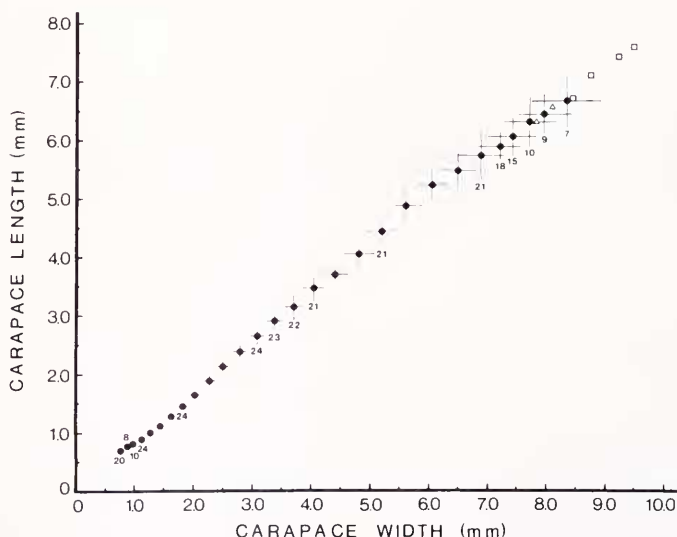

FIGURE 2. Relative growth of the carapace of *Dissodactylus primitivus*. Each circle represents a mean measurement for one instar up to instar 28. Number of observations per instar is shown; if not given, number equals that of adjacent instar. Vertical and horizontal lines are standard deviations. Additional points are given for the lone male (△) and the lone female (□) which surpassed instar 28.
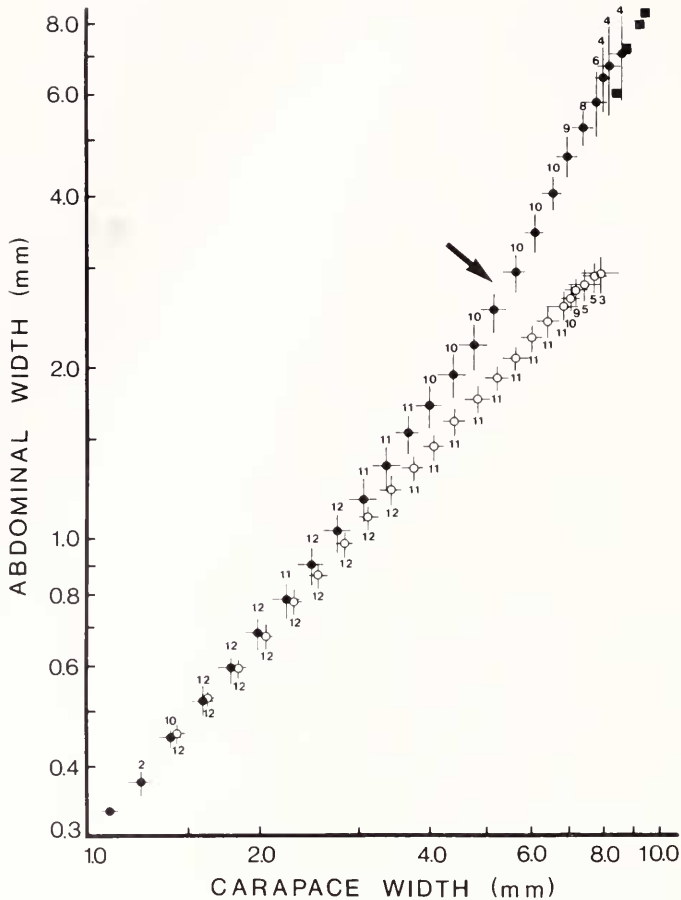
FIGURE 3. Relative growth of the abdomen of *Dissodactylus primitivus*. Open symbols represent males, closed symbols females. Each circular symbol is a mean measurement for one instar, with the number of observations given. Vertical and horizontal lines are standard deviations. Four additional square symbols represent instars 29 to 32 of one female individual in which molt of instar 28 to 29 represents a pubertal molt. Arrow between instars 19 and 20 indicates point of transition from early to late prepubertal growth.

Intermolt period

Intermolt period (INTMT) and carapace width (CW) best fit a semi-log relationship (Fig. 4), as follows:

Males: $\log \text{INTMT} = 0.127 \cdot \text{CW} + 0.722$ ($r^2 = 0.875$, N = 260)

Females: $\log \text{INTMT} = 0.110 \cdot \text{CW} + 0.767$ ($r^2 = 0.835$, N = 250)

Slopes of these regressions were significantly different ($F = 15.66$, $P = 0.0001$).

A similar relationship was found between intermolt period and successive post-larval instar numbers:

Males: $\log \text{INTMT} = 0.038 \cdot \text{INSTAR} + 0.671$ ($r^2 = 0.899$, N = 293)

Females: $\log \text{INTMT} = 0.034 \cdot \text{INSTAR} + 0.703$ ($r^2 = 0.859$, N = 279)

Slope differences between sexes were significant ($F = 10.03$, $P = 0.0002$). Although these appear negligible, intermolt periods become significantly different at higher instars. For example, at instar 7 calculated intermolt periods were 8.6 days for males, 8.7 days for females and at instar 27 corresponding periods were 49.8 and 41.8 days. Regression equations for intermolt period and carapace width (above) yielded similar differences.

Growth increments

Significant linear correlation was obtained between percent growth increments and carapace width or instar number using log-linear and linear-linear regressions, as obtained for other Crustacea by Maucheline (1977). Non-transformed regressions were chosen here, however, because of the significantly better fit for both sexes. Plotting percent increment (P-INCR) against carapace width (CW) (see Fig. 5) resulted in the equations:

Males: P-INCR = $-1.464 \cdot$ CW $+ 14.894$ ($r^2 = 0.709$, N = 256)

Females: P-INCR = $-1.194 \cdot$ CW $+ 14.328$ ($r^2 = 0.734$, N = 248)

An F value of 13.16 indicated a difference of slope between sexes ($P = 0.0001$). Semi-log regression of the same data gave r^2 values of 0.605 and 0.698, respectively. A similar relationship was obtained between percent increment and successive instar
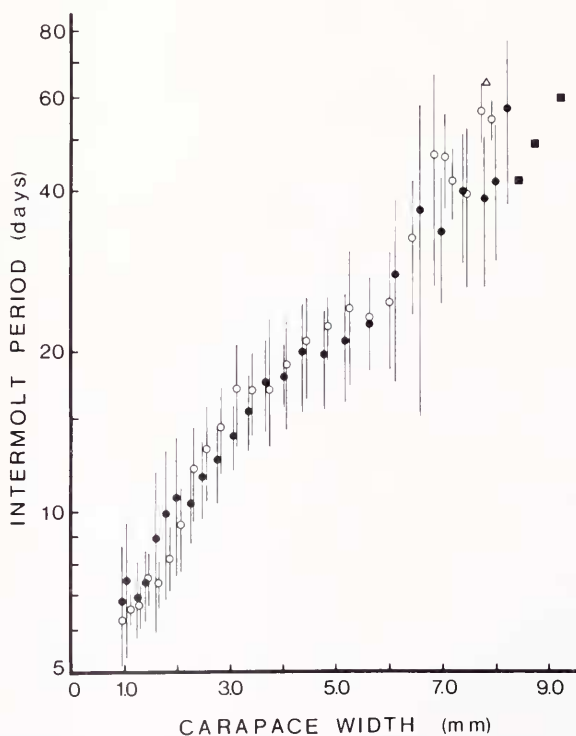

FIGURE 4. Intermolt periods and carapace widths of *Dissodactylus primitivus*. Symbols as in Figure 3. Vertical bars represent standard deviations. Additional intermolt periods are given for one male (△, instars 29–30) and one female (■, instars 29–32).
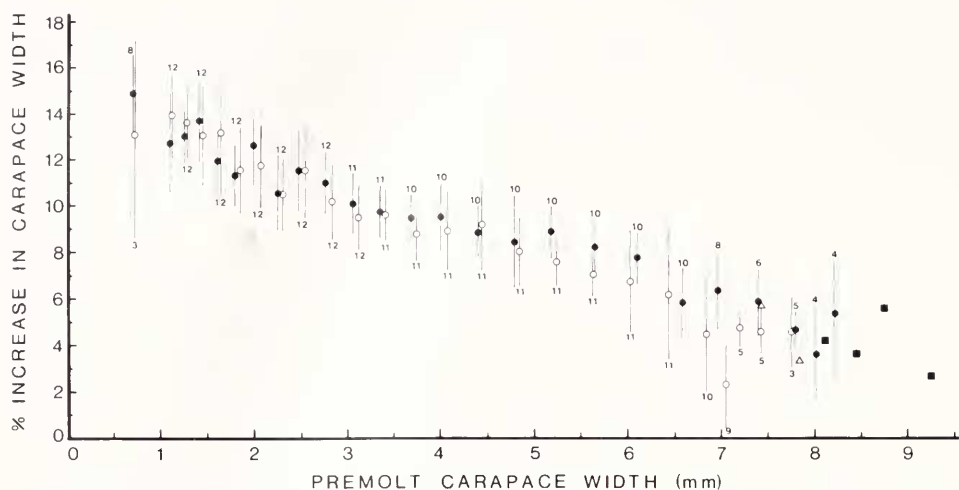
FIGURE 5. Carapace growth of *Dissodactylus primitivus* males and females as a percent increment based on premolt width. Symbols as in Figure 3.

numbers:

Males: P-INCR = $-0.449 \cdot$ INSTAR + 15.758   (r^2 = 0.707, N = 256)

Females: P-INCR = $-0.382 \cdot$ INSTAR + 15.214   (r^2 = 0.729, N = 248)

Semi-log regression resulted in lower r^2 values (0.556 and 0.664, respectively).

Growth rate

The relationship between carapace width (CW) and age (days after hatch) is shown in Figure 6. For both sexes the data best fit a power function.

Males: log CW = $0.739 \cdot$ log AGE $-$ 1.053   (r^2 = 0.970, N = 268)

and

log AGE = $1.311 \cdot$ log CW + 1.445

Females: log CW = $0.791 \cdot$ log AGE $-$ 1.172   (r^2 = 0.952, N = 260)

and

log AGE = $1.203 \cdot$ log CW + 1.512

Slopes of male and female regressions were significantly different (F = 14.46, P = 0.0002). This seems to be primarily explained by the decreased carapace growth of older males. This is in agreement with observations that *D. primitivus* adult males are smaller than females in the wild. Growth in carapace width of individual females which passed through pubertal molts showed no significant departure from the curve (square symbols, Fig. 6). Thus, in contrast to abdominal width, carapace width and intermolt period does not seem to change abruptly at the onset of sexual maturity.
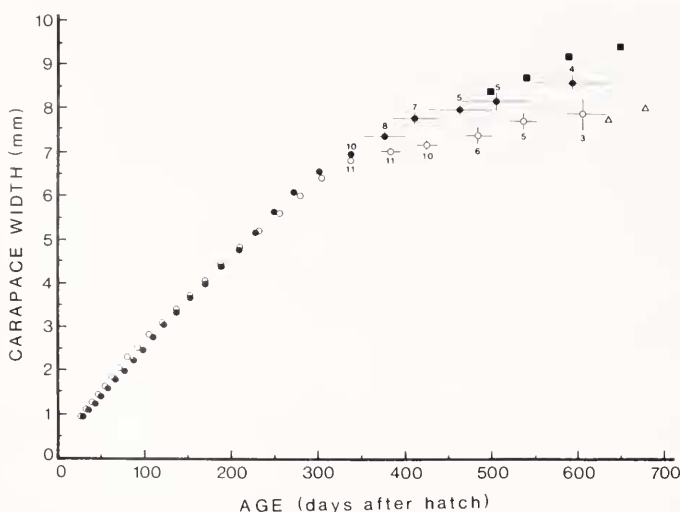
FIGURE 6. Growth rate of *Dissodactylus primitivus* males and females. Open and closed circles represent mean measurements of instars 3 to 28 for males and females, respectively. Additional points are given for one male (△, instars 29 and 30) and one female individual (■, instars 29 to 32). Vertical and horizontal lines represent standard errors for instars 24 to 28, with number of observations given. For remaining data points number of observations as in Figure 5.

Other relationships

Growth of Crustacea can also be described by weight (Hewett, 1974). During this study weights were not recorded. Kurata (1962) and Maucheline (1977) pointed out that an analogous relationship to weight can be obtained by substituting the cube of body size measurements (carapace width or length) for weight. This holds true only in the absence of marked allometric growth. Studies of several Crustacea, including the spiny lobster *Jasus lalandei* (Fielder, 1964) and the king crab *Paralithodes camtschatica* (Weber, 1967) indicate that, for practical purposes, weight varies in direct proportion to the cube of carapace length ($y = ax^3$). On this basis several linear relationships have been reported.

Kurata (1962) showed a linear relationship between intermolt period and the cube of body length for several Crustacea. Regressing *D. primitivus* intermolt period (INTMT) against the cube of carapace width (CW^3) resulted in a linear relationship:

Males: $INTMT = 0.092 \cdot CW^3 + 9.934$ ($r^2 = 0.775$, $N = 260$)

Females: $INTMT = 0.070 \cdot CW^3 + 10.436$ ($r^2 = 0.717$, $N = 250$)

Although the difference between slopes was very small, it was statistically significant ($F = 28.57$, $P = 0.0001$).

In the common lobster, *Homarus vulgaris*, Hewett (1974) found that the log of growth increment, in weight, was linearly related to log of body weight. Maucheline (1977) obtained an analogous relationship for *H. americanus* by cubing log of increment (log $INCR^3$) and carapace length (CL^3) data. Using the same approach for *D. primitivus* with carapace width, a significant relationship can be obtained for the first 21 instars; for later instars there is significant deviation.

Males: $\log \text{INCR}^3 = 0.584 \cdot \log \text{CW}^3 - 2.460$ ($r^2 = 0.667$, N = 211)

Females: $\log \text{INCR}^3 = 0.689 \cdot \log \text{CW}^3 - 2.548$ ($r^2 = 0.865$, N = 207)

The difference in slope was significant ($F = 9.45$, $P = 0.0023$).

Hewett (1974) demonstrated that the log of body weight was linearly related to log of age. The analogous relation of the log of carapace width cubed ($\log \text{CW}^3$) and log of age for *D. primitivus* was:

Males: $\log \text{CW}^3 = 2.218 \cdot \log \text{AGE} - 3.158$ ($r^2 = 0.970$, N = 268)

Females: $\log \text{CW}^3 = 2.374 \cdot \log \text{AGE} - 3.517$ ($r^2 = 0.952$, N = 260)

The slopes were significantly different ($F = 14.46$, $P = 0.0002$).

DISCUSSION

In this study the highest death rate occurred during the short span of larval life, where it was due to imperfect molting. In the wild such high mortality has been observed but was attributed mostly to heavy predation (Warner, 1967). Data obtained in the laboratory suggest that mortality in the sea may also be at least partially caused by failure in molting. Post-larval deaths, although fewer, were also mostly attributed to molting difficulties similar to those described by Fielder (1964) for the spiny lobster, *Jasus lalandei*. Fielder noted that swelling of the new integument sometimes occurred before withdrawal from the old exoskeleton was accomplished. Thus, the time to complete a molt is limited. Similarly, either the appendages or the abdomen of *D. primitivus* could sometimes not be freed. Without exception all individuals in this study (larvae and post-larvae) molted at night and those which had not completed molting by daybreak died.

Changes in form of carapace occur in pinnotherid crabs symbiotic with pelecypods. *Pinnotheres ostreum* (Christensen and McDermott, 1958) and *Fabia subquadrata* (Pearce, 1966a), for example, have hard, flattened, or square invasive stages, respectively, followed by more convex or oval pre-swarming stages. These differences between stages are specialized adaptations to a life within molluscan hosts. In both *D. crinitichelis* (Telford, 1978a) and *D. primitivus*, carapace growth is isometric, length–width ratios not significantly changing over the size range. Such carapace growth is typical but not universal in crabs (Warner, 1977). Barnes (1968) found an increase in width over length during growth of some sentinel crabs (Ocypodidae). This change in shape is a functional adaptation to side-burrowing (Warner, 1977). Claims for various growth patterns are often made without adequate statistical testing (Brown and Davies, 1972). Re-examination of Barnes' data, for example, showed that only some of the species in fact had linear relationships with intercepts significantly different from zero (allometry). Finney and Abele (1981), studying growth in a xanthid crab symbiotic with corals, found that the carapace of males and non-ovigerous females increased in length over width, but ovigerous females showed isometric growth. Without suitable statistical tests such differences would not have been apparent.

Sexual dimorphism in *D. primitivus* is most apparent in abdominal growth. Males and females can be distinguished by abdominal widths during juvenile stages long before sexual maturity is reached. The increased abdominal growth for females is necessary in reproduction, where the abdomen acts in conjunction with the sternum as a cover to an incubation chamber. The abdomen of *D. primitivus* males grows more or less isometrically, whereas females show positive allometry. In other crabs (MacKay, 1943; Haley, 1973; Hartnoll, 1974; Finney and Abele, 1981)

female abdominal growth cannot be explained by simple allometry with a single straight line. Two phases can be recognized: the first of high positive allometry (pre-puberty), followed by one of low positive allometry (post-puberty). When analyzing a population *en bloc*, the change in allometry is presumptive evidence of a pubertal molt, a sudden large increase in abdominal width indicative of sexual maturity (Haley, 1969; Finney and Abele, 1981). Data of *D. primitivus* suggest two phases leading to sexual maturity (Fig. 3). The first is a juvenile phase of low positive allometric growth, followed by one of stronger abdominal growth. It is during the latter phase that the species is capable of maturing, for it is here that pubertal molts for two females were observed (Fig. 3). Sexual maturity is thus not reached at a constant size (nor at a fixed instar) but varies from individual to individual. Hence the observed population inflection cannot be explained as a simple one-step process: a change of growth also occurs before the pubertal molt. Prior to successful reproduction various secondary sexual characters appear, and the internal reproductive system must become functional (Finney and Abele, 1981). The phase of increased abdominal growth probably marks one or more of these physiological changes before the pubertal molt. Haley (1973) observed two similar growth phases leading to sexual maturity in *Ocypode ceratophthalmus*. In that crab the second phase has been specifically attributed to increased growth of the fourth abdominal segment. After their pubertal molts, growth of the two *D. primitivus* female individuals decreased. Post-pubertal growth appears to represent a separate phase of abdominal development but has not been fully analyzed due to insufficient data. Abdominal growth in *Pinnotheres pisum* (Needham, 1950) also did not follow simple allometry. Needham fitted the data onto progressively higher polynomial functions in order to arrive at a continuous and accurate description of growth.

Compared to estimates for other Crustacea such as *Cancer magister* (Butler, 1961), the number of observed molts for *D. primitivus* to reach adult size seems high. On the other hand, the shrimp *Crangon crangon* (Meixner, 1969), had 23–25 post-larval molts before reproduction in females, and 22–25 in males. This is similar to *D. primitivus*, where pubertal molts occurred after 26 and 29 instars, respectively.

Growth of Crustacea can be described in terms of duration of successive intermolt periods, which increases in most Crustacea as the organism ages (Maucheline, 1977). There are some notable exceptions, and possibly there are also differences between sexes. Studies by Reaka (1979) on coral-dwelling stomatopods and Miller *et al.* (1977) on marine copepods seem to indicate a more or less constant molting frequency (isochronal development). In decapod Crustacea a difference in intermolt periods of equal-sized males and females was found by Meixner (1969) in *Crangon*, where large females molted more frequently. Large females of *D. primitivus* similarly showed shorter intervals between molts than did equal-sized males.

Duration of intermolt period is affected by several environmental factors, but especially by temperature (Lasker, 1966). Kurata (1962) showed that temperature variation significantly alters terms of the regression equations. In this study of *D. primitivus*, laboratory temperature was stable and similar to the natural environment.

Changes in size have commonly been analyzed in two ways. The widely accepted regression of post- on pre-molt body size (Hiatt, 1948), has recently been criticized (Maucheline, 1976, 1977) on theoretical grounds and because it presupposes constancy of growth increments. Alternatively, growth can be analyzed by plotting

absolute size increase or percent increase against body size (Farmer, 1973). The former usually results in a positive relationship. However, the latter results in a negative relationship, percent increments decreasing with size. In place of body size, successive instar numbers may also be used with similar results.

Decreasing percent increments and body size can be fitted to straight lines (Maucheline, 1977) for many Crustacea, including lobsters (Fielder, 1964; Thomas, 1965)) and crabs (Warner, 1967; Turoboyski, 1973). Such a relationship was found for *D. primitivus*, but the mean growth increments were relatively small. In early stages they ranged from about 14 percent to near zero growth in later instars. Results here are comparable with such other pinnotherids as *Pinnotheres ostreum* (10% between instar 1 to 2, Sandifer, 1972), and *Pinnixa faba* and *P. littoralis* (about 20%, Pearce, 1966b). Larger species, such as *Cancer magister* (Butler, 1961), have considerably higher percent increments (43%, instar 1 to 2).

Growth increments, however, do not always fall on a single straight line. For the amphipod *Parathemisto gaudichaudi* Sheader (1981) showed two distinct phases: a juvenile phase of rapidly decreasing growth, followed by a maturing phase with more gradually decreasing growth. Ostracods and calanoid copepods are also believed to be exceptions (Maucheline, 1977). Miller *et al.* (1977) showed near constant percent growth increments for marine copepods.

Data for growth rates have been obtained in a number of ways (Burkenroad, 1950) including growth of tagged individuals, change in size-frequency distribution, and laboratory maintenance. Laboratory culture was chosen in this study because development of individuals could be followed for prolonged periods in controlled environments. While techniques differ, many studies have come to the conclusion that growth decreases with time, irrespective of size or species [Farmer (1973), and Hewett (1974) for lobsters; Meixner (1969) for shrimps; and Warner (1967), Weber (1967), and Bennet (1974) for crabs]. The data obtained from culture of *D. primitivus* support the above observation and fit a power function. This relationship has been indirectly estimated for other Crustacea (Warner, 1967) but never demonstrated by continuous long-term culture of individuals. Growth rates of *D. primitivus* are different for males and females (Fig. 6). During the first year these differences are slight, thereafter growth increments for males decrease (see equations for Fig. 5) and intermolt periods increase (see equation for Fig. 4). Thus the smaller size of males can be explained by a slower growth rate rather than by a cessation of molting. In wild populations of *D. primitivus* the same difference between the maximum sizes of males and females was observed.

Differences in growth rates between sexes are known for other Crustacea, most of which have larger males than females. In this respect *D. primitivus*, as other pinnotherids, is an exception. Size differences between sexes in pinnotherids living inside molluscs or burrows of polychaetes, such as *Pinnotheres ostreum* (Christensen and McDermott, 1958) and *Pinnixa cylindrica* (McDermott, 1981), have been attributed to differences in life history. Only male crabs may leave for another host in order to locate additional mates and thus become more vulnerable to predation. This results in fewer males reaching a larger size. In *D. primitivus*, which is an external parasite, it is likely that both male and female crabs move from host to host, just as in *D. crinitichelis* (Telford, 1978b). Larger *Dissodactylus* females may be necessary for the production of enough eggs to ensure propagation of the species.

Bennet (1974) suggested the use of a linear relationship between percent molt increment and premolt weight of the crab *Cancer pagurus*. Applying the cubed carapace length transformation, Maucheline (1977) found this relationship to be unsatisfactory at extremities of size for *Homarus americanus*. The data here also

fit only a small part of the size range, and the relationship was rejected. However, a significant linear relationship was obtained with these parameters using a log–log transformation. For *Homarus vulgaris* Hewett (1974) obtained a significant linear correlation between log of intermolt period and the cube root of body weight. As Maucheline (1977) showed, this is analogous to log of intermolt period and body size (CW or CL), a relationship which has been demonstrated here.

ACKNOWLEDGMENTS

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